Environmental complexity, life history, and encephalisation in human evolution

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Abstract

Brain size has increased threefold during the course of human evolution, whilst body weight has approximately doubled. These increases in brain and body size suggest that reproductive (and, therefore, evolutionary) rates must have slowed considerably during this period. During the same period, however, environmental heterogeneity has increased substantially. A central tenet of life-history theory states that in heterogeneous environments, organisms with fast life histories will be favoured. The human lineage, therefore, has proceeded in direct contradiction of this theory. This contribution attempts to resolve this contradiction by recourse to Godfrey-Smith's *Environmental Complexity Thesis*, which states that the function of cognition is to enable the organism to deal with environmental complexity. It is suggested that among slowly reproducing organisms the behavioural flexibility provided by advanced cognitive abilities is a fundamental component of adaptation to heterogeneous environments. In the human lineage this flexibility is manifest particularly in the increasing complexity of material culture.

Keywords: cognition, evolution, dispersal, complexity, hominin.

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1. Introduction

This contribution addresses the relationship between environmental heterogeneity and human evolution via an examination of some of the central themes of Godfrey-Smith's (1996) Environmental Complexity Thesis (henceforth ECT). This thesis states that the function of cognition is to deal with environmental complexity, where complexity is understood as a synonym for heterogeneity. The paper begins by examining parallels to the ECT in evolutionary anthropology, where interest in the relationship between palaeoenvironmental change and hominin adaptation has a long history. The recent shift from hypotheses based on long-term climatic change to those based on shorter-term climatic variability brings evolutionary anthropology considerably closer to the ideas examined in *Complexity and the Function of Mind in Nature* (Godfrey-Smith 1996; henceforth CFMN). The relationship between human encephalisation and climate is also a burgeoning area of research; this is examined here within a broader consideration of the hominin life-history suite of which brain size is a central component.

Using a combination of empirical analyses and theoretical models, it is demonstrated that environmental complexity has increased considerably over the past five million years, and that this environmental trajectory is paralleled by 1) a marked increase in hominin brain size over at least the last three million years, and 2) a considerable decrease in hominin reproductive rates over the same period. The hominin lineage thus contradicts a fundamental tenet of life-history theory: that increasingly disturbed environments should select for *increasing* reproductive rates. Decreasing reproductive rates in the face of increasing environmental complexity produced a considerable deficit in the ability of the hominin lineage to track changing environmental conditions; a deficit that was compensated for, it is argued, via an increased reliance on phenotypic plasticity as a means of adapting to such conditions. Phenotypic plasticity is defined broadly so as to include both behaviour and material culture, and it is argued that the cultural transmission of the latter, facilitated by the enhanced cognitive abilities conferred by encephalisation, is the key to understanding the hominin adaptation.

The paper concludes with a discussion of some of the most important operational differences between biological and cultural evolution, and maps the broad stages of hominin evolution onto Godfrey-Smith's (1996) distinction between individual and population-level complexity. It is suggested that cultural manifestations of plasticity, by relaxing some aspects of direct selection on the genotype, led to increased genotypic diversity in populations of ancestral humans. In the terms of CFMN, this resulted in situations in which individuals were plastic, and therefore complex; more importantly, however, this scenario raises the generic possibility that individual complexity will lead automatically to population-level complexity under certain conditions.

2. Human Evolution and the ECT

In the same year that CFMN was published, Potts published *Humanity's Descent: the Consequences of Ecological Instability* (Potts 1996), a book that considered a closely related but more specific hypothesis: that inconsistency in adaptive conditions caused by substantial climatic fluctuations over

time “eventually caused habitat-specific adaptations to be replaced by structures and behaviours responsive to complex environmental change” (Potts 1998:81). The *Variability Selection Hypothesis* (henceforth VSH) was explicitly formulated to explain the appearance of key adaptations in the hominin lineage, many of which may be viewed as responses to increasing environmental heterogeneity; in many ways, therefore, the VSH is the evolutionary anthropologist’s ECT. While Potts is not concerned solely with explaining the function of cognition, hominin encephalisation is viewed as one of the central trends emerging from adaptation to fluctuating environments over geological timescales. Indeed, he states that a large brain “effective in processing external data and generating complex cognitive responses” (Potts 1998:85) would have been a primary asset in dealing with climatic instability.

Before detailing some of the analyses prompted by the VSH within evolutionary anthropology, it is necessary to briefly review research on the relationship between palaeoclimatic change and human evolution prior to its appearance. Much of this research focused on variants of the ‘savannah hypothesis’, suggesting that the divergence of the hominins from an essentially chimpanzee-like last common ancestor was related to a perceived ecological difference between the closed forest environments of modern chimpanzees and the open grassland habitats of many extant human hunting and gathering groups. The standard account proceeded as follows: the opening of the savannah led to the loss of arboreal adaptations and the evolution of bipedalism, which freed the hands for making and using tools; such tools facilitated an increase in the consumption of animal protein, which in turn led to the growth of larger brains; our encephalized ancestors then proceeded to develop symbolism, language, and various cultural and religious customs in no particular order.

It has since become clear, however, that chimpanzees are capable of inhabiting savannah environments (e.g. Pruetz et al. 2002), that they are adept tool users (e.g. McGrew 1992), and that they routinely hunt (e.g. Watts and Mitani 2002) – sometimes with tools used specifically for the purpose (e.g. Pruetz et al. 2007); it is equally clear that extant human hunter-gatherers are not confined to savannah environments (e.g. Hart and Hart 1986). It now seems increasingly likely that some of the first bipedal hominins inhabited forested environments (e.g. White et al. 2009), thus severing the link between the bipedalism and the savannah. Finally, the notion that the last common ancestor was essentially a chimpanzee is about as sensible as the notion that the last common ancestor was essentially a modern human. The link between increasing diet quality and encephalisation remains likely, albeit via a rather more sophisticated argument (e.g. Aiello and Wheeler 1995).

Undoubtedly the most severe blow to this and other ‘habitat-specific’ hypotheses, however, has been the publication of increasing numbers high-resolution, long-term records of prehistoric environmental change. Though the general trend towards cooler, drier environments upon which the savannah hypothesis was based is still apparent over the past five million years in these records, they also display convincing evidence that this trend plays a subsidiary role to the marked increase in variability seen over the same period (Potts 1996, 1998; Grove 2011a, 2011b, 2012a, 2012b). Since the empirical demonstration that the Earth’s glacial cycles are governed at geological timescales by orbital effects on the strength of solar insolation (Hays et al. 1976), the mechanism behind this variability has also become increasingly clearly understood (e.g. deMenocal 2004). The three major orbital cycles of eccentricity, obliquity, and precession, with periods of ~100 ka, ~41 ka, and ~21 ka respectively, have varied in their relative contributions to global insolation patterns over the past

five million years. Crudely speaking, the increasing dominance of first the obliquity cycle (after ~3 Ma) and then the eccentricity cycle (after ~1 Ma) is responsible for both the decreasing frequency and increasing amplitude of palaeoclimatic oscillations over this period (e.g. deMenocal 2004). Thus the weight of evidence now strongly suggests that climatic variability, rather than climatic change, was the predominant abiotic force responsible for the adaptive radiation of the hominins (Grove 2011b); hypotheses linking human evolution and palaeoclimatic variables must therefore focus their explanations on the effects of this variability.

In this context, the emergence of the VSH (Potts 1996) has prompted a series of related hypotheses that link elements of palaeoclimatic variability with particular aspects of hominin evolutionary history. Of particular note are Kingston's 'shifting heterogeneity model' (Kingston 2007) and the 'pulsed cimate variability hypothesis' of Trauth and colleagues (e.g. Maslin and Trauth 2009). The former links variation in selective pressures caused by precession effects in equatorial Africa with shifts in seasonality, vegetation physiognomy, and faunal distribution patterns. It is predicted that these shifts would in turn lead to vicariance, increased intra-specific variation, and ultimately speciation in hominin species exploiting the affected flora and fauna. The latter hypothesis also links the evidence for precessional pacing of palaeoclimatic change at low latitudes with population vicariance and allopatric speciation, but argues that lake formation and disappearance in the topographically complex setting of the East African Rift System would have amplified variations in precipitation at shorter temporal scales. The 'amplifier lakes' of Trauth and colleagues (2010) would have acted as both resources for and barriers between hominin populations, leading to pulses of population fission and fusion during each precession cycle.

3. Climatic Variability, Encephalisation, and Intelligence

Of relevance to the current study is a subset of the research into the effects of climatic variability on human evolution that explicitly considers the environmental correlates of encephalisation. Ash and Gallup (2007), for example, indexed temporal climatic variability by the standard deviation of a long-term palaeoclimatic record per 100 ka and correlated this index with hominin endocranial capacities gathered from the literature. At this crude scale, variability explained 52% of the variation in endocranial capacity. The distance from the equator at which each cranium was recovered, used as an index of seasonal variability, explained 22% of the variance in a separate analysis. Grove (2012), using an expanded endocranial database, found that the amplitudes of the individual orbital cycles and the absolute first derivative of the palaeotemperature curve together explained 59% of the variance. Such studies provide a counterpoint to those examining correlations between brain size (or components thereof) and proxies for social complexity (e.g. Dunbar 1998). There is no need, however, to present environmental and social hypotheses of encephalisation as being mutually exclusive. On the current balance of evidence, it appears highly likely that social complexity was a significant driver of hominin encephalisation; however, it is also highly unlikely to have been the only such driver. Relationships between environmental variability and encephalisation found across multiple taxa (reviewed by Grove 2012) clearly demonstrate the importance of this relationship.

Though studies on fossil hominins are restricted to the measurement of crude brain sizes (or endocranial capacities, which are essentially equivalent (e.g. Aiello and Dunbar 1993)), studies of contemporary humans and other animals often employ behavioural indicators of intelligence. It is useful, therefore, to ask whether brain size itself is a useful index of cognitive abilities. Within

evolutionary anthropology, brain size and cognitive ability have become almost synonyms; it is important, therefore, that recent research in other disciplines has provided explicit empirical support for this long-standing assumption. Shultz and Dunbar (2010) demonstrate that the performances of 46 primate species on 8 separate executive function tasks are not only inter-correlated, but that each also correlates positively with brain size. Reader and colleagues (2011) employ data on various cognitive measures including frequencies of innovation and social learning and demonstrate strong positive associations between each of these measures. Via principal component analyses they develop a measure of general, species-specific intelligence, and find that this composite measure correlates positively with brain size across 62 primate species. Taken together, these analyses demonstrate that overall brain size acts as a reasonable index of cognitive abilities. The high inter-correlation of various test scores further suggests that there is no need to posit the existence of specialised, task-specific learning mechanisms or 'modules' in the primate brain.

4. Body Size, Encephalisation, and Life History

Although encephalisation confers considerable benefits in terms of cognitive ability, it also entails substantial costs. These costs are rooted in two fundamental life history trade-offs: at what point in an animal's life should it switch from investing in somatic growth to investing in reproduction, and should it invest in quality or quantity of offspring? That there might be optimal solutions to these questions, and that the apportioning of additional energy to one strategy or the other might therefore constitute an adaptive response, was first suggested by Lack (1954). Only with MacArthur and Wilson's (1967) *r*- and *K*-selection theory, however – or perhaps with Pianka's (1970) exposition of the theory in more general terms – did life history theory assume something like its current form. The canonical statements of r / K theory are phrased in terms of density dependence and its effects on reproductive strategies. Population sizes in species experiencing temporally heterogeneous environments might periodically decline; if these declines are 'catastrophic', mortality may be independent of fitness, and the resulting vacuum will be filled by those individuals that can reproduce the fastest. The population will frequently operate below carrying capacity, meaning that inter-specific competition for resources will rarely be a constraint. In such a situation, individuals that maximise their per capita growth rate (*r*), sacrificing quality for quantity, will prevail. In more static environments, however, population sizes will be relatively stable and usually close to carrying capacity. At this *K*-selected end of the spectrum, therefore, "competition is keen and the optimal strategy is to channel all available matter and energy into maintenance and the production of a few extremely fit offspring" (Pianka 1970:593).

Though the *r* / *K* version of life history theory has been criticised in some areas, it remains exceptionally useful as a heuristic dichotomy. Ross (1992), for example, employed the theory when studying intrinsic rates of increase in primates, demonstrating that variable, dry, and hot climates are associated with life histories towards the *r*-selected end of the spectrum. Subsequent theory has moved towards an understanding that density dependence is not the only factor conditioning life history strategies, yet the continuum between 'fast' and 'slow' life histories continues to be usefully employed. A particular strand of this research has focused on the association of body size with life history variables, supporting the initial assertion (MacArthur and Wilson 1967; Pianka 1970) that larger body sizes are indicative of *K*-selection (e.g. Western 1979; Harvey and Clutton-Brock 1985).

The association between large body size and slow reproductive rates is thus well established. The majority of papers examining this relationship, however, do not explicitly extend the logic from slow rates of reproduction to slow rates of evolution. The effects of life history on evolutionary rates arguably provide a better explanation of the recurring association between 'fast' life histories and fluctuating environments than do their effects on reproductive rates *per se*. Assuming that recombination is a primary factor in generating genetic variance in sexually reproducing populations, it stands to reason that rapidly reproducing animals would generate more variation per unit time than slowly reproducing animals. This would produce more 'raw material' for natural selection to act upon, thus potentially increasing evolutionary rates. This logic suggests that species with fast life histories will be favoured in fluctuating environments because their increased production of genetic variation is more likely to lead by chance to genetic variants that are beneficial in the newly disturbed environments they encounter. By contrast, slowly reproducing species produce less genetic variation and may therefore be forced to deal with environmental fluctuation through non-genetic means.

It has been repeatedly demonstrated that evolutionary rate variation correlates with life history variables such as generation time (e.g. Bromham et al. 1996; Nabholz et al. 2008). However, correlations between body size and both generation time and metabolic rate have somewhat clouded the picture as to the true driver(s) of evolutionary rates, leading to two major hypotheses. The generation time hypothesis follows from the logic outlined above, whereby shorter generation times lead to faster evolution due to higher rates of recombination and more DNA replication errors per unit time. By contrast, the metabolic rate hypothesis suggests that most genetic variation arises through mutations caused by free radical damage; since free radical production is a by-product of metabolism, evolutionary rates should co-vary with metabolic rates. Since both generation time and metabolic rate are negatively correlated with body size, it is hard to tease these two theories apart. What is clear, however, is that larger organisms evolve more slowly than smaller organisms, regardless of the hypothesis considered more likely.

There is, however, an additional factor that some researchers have suggested is more important than body size in determining reproductive rates. Recent papers by Isler and Van Schaik (2009a, 2009b) suggest that brain size, not body size, is the key determinant of a series of life history variables including the intrinsic rate of increase, r_{max}. This work revises and extends the Expensive Tissue Hypothesis (henceforth ETH), proposed by Aiello and Wheeler (1995) to account for the evolution of large brains in the hominin lineage. The ETH proposes that increases in volume of metabolically expensive brain tissue were offset by decreases in the volumes of the equally expensive tissues involved in digestion, and thus that encephalisation in the hominins was only possible due to increases in dietary quality. Retaining the focus on the metabolic expense of brain tissue, Isler and Van Schaik (2009a) argue that the cost of encephalisation is apparent via reduced fertility rates. They further suggest (Isler and Van Schaik 2009b) that brain size, not body size, is the best predictor of the intrinsic rate of increase.

Although Pianka's famous table listing the correlates of *r*- and *K*-selection (Pianka 1970:593) does not mention brain size, the relationship between *K*-selection and larger brain size follows logically from the close correlation between body size and brain size, and is therefore widely accepted. Whether body size, brain size, or some combination thereof provides the best predictor of reproductive rates remains contentious. It is likely that brain size plays a greater role in lineages or

species that have unusually large brain to body size ratios, indicating that predictive equations are unlikely to be uniform across taxa and that the most robust methods will involve multiple regressions or composite analyses that take both variables into account. Such an approach was in fact suggested over 50 years ago in a series of important papers by Sacher and Staffeldt (Sacher 1959, 1978; Sacher and Staffeldt 1974). Using a similar logic to Isler and Van Schaik (2009b), Sacher (1959) argued that, because the growth rate of brain tissue is slower than that of other organs, brain size might be a key restriction on the time taken to reach maturity and could thus be expected to influence overall rates of reproduction. Sacher and Staffeldt demonstrated that both brain size and body size influence rates of foetal growth (Sacher and Staffeldt 1974) and lifespan (Sacher 1978), whilst a similar pattern was shown by Millar (1977) for postnatal growth. Western (1979) argued that general allometric equations relating both body size and brain size to life history characteristics should be employed in order to gain the most accurate results.

It is thus clear that both increasing body size and increasing brain size entail considerable costs in terms of reproductive rates; following the logic above, these costs should also be manifest in the reduction of evolutionary rates. Critically for the current paper, reduced evolutionary rates will impair a lineage's ability to track a heterogeneous environment through genetic evolution. The evolution of the hominins since the last common ancestor with chimpanzees, and particularly the trajectory followed by our own genus, thus poses something of a paradox; since the time of the gracile australopithecines body size has increased by a multiple of two, and brain size by a multiple of three, yet this has occurred against a backdrop of increasing climatic and environmental heterogeneity.

5. The elements of the argument

The following sections aim to divide this paradox into its constituent parts, to provide evidence for each, and to document their likely effects on human evolution. Following this, a solution to the paradox is postulated, suggesting that encephalisation provides levels of plasticity sufficient to allow 'slow' species to accommodate environmental change via cultural means.

5.1. Climatic heterogeneity has increased during hominin evolution

Examination of long-term palaeoclimatic datasets demonstrates that climatic heterogeneity has increased dramatically over the past five million years. Whilst this is clear simply from plotting these datasets over time, it is useful here to formally quantify this increase. The Shannon index, developed to quantify the entropy of a signal (Shannon 1948) and routinely used as a measure of the diversity of species in an ecological assemblage, provides an equally valuable measure of the heterogeneity of a climatic variable over time. To calculate changes in this index over time, a moving window approach was developed that first produces a normalized histogram of the values that a palaeoclimatic variable assumes during a given time window, then calculates the diversity of climatic values as $H = \sum_{i=1}^{n} -p_i \ln p_i$, where p_i is the proportion of values falling within bin i and n is the total number of bins required to characterise the full dataset. Figure 1 plots an example of this procedure using the LR04 stack (Lisiecki and Raymo 2005), an average of 57 globally distributed benthic $\delta^{18}O$ records of global ice volume and deep ocean temperature that extends over the past 5 million years. Figure 1a shows the normalised histograms arranged vertically, per 5 thousand year interval, and Figure 1b shows the Shannon index at the same scale.

Figure 1a demonstrates both the long-term decrease in temperatures during this period (higher $\delta^{18}O$ values indicate lower temperatures) and the increasing spread of values represented during a given interval. Figure 1b explicitly demonstrates the increase in climatic heterogeneity over time. It is useful to note that, whilst the overall trajectory is one of increasing heterogeneity, there is an early heterogeneity peak around 2.5 million years ago. This is caused by an erratic pulse of colder climatic conditions associated with the onset of northern hemisphere glaciation, when large ice sheets first spread over the northern continents, and has been linked to the beginnings of the central hominin adaptive radiation comprising the origins of the genus Homo (e.g. Grove 2011a, 2011b). Nonetheless, the overall picture suggests a marked increase in climatic heterogeneity over the past 5 million years, and this is likely to have had considerable implications for the evolutionary trajectories of various species during this period.

5.2. Reproductive rates have decreased during hominin evolution

There have been numerous attempts to reconstruct the life histories of the hominins (e.g. Robson and Wood 2008). Since the key variables cannot be directly measured in extinct animals, the dominant approach involves recourse to well-established relationships between those variables and body mass. The body masses of extinct hominins can be calculated via regression equations relating body mass to femoral head diameter in extant primate samples (e.g. McHenry 1992). A more recent approach employs multivariate relationships that use multiple skeletal elements for prediction based on relationships established in a large sample of modern humans of known body mass (Grabowski et al. 2015). Of particular interest has been the relationship between body mass and the maximum intrinsic rate of increase per individual, $r_{\max}$. $r_{\max}$ is a useful measure because it subsumes variation in the three most critical variables – female age at first reproduction, maximum birth rate of females, and the number of female offspring born per year. Ross (1988, 1992) calculated $r_{\max}$ for a broad sample of primate species, and demonstrated a highly significant negative relationship between this variable and body mass. This result is in accordance with earlier findings from a wide array of taxa (e.g. Henneman 1983), and with subsequent studies that emphasize the relatively 'slower' life histories of larger organisms (e.g. Charnov and Berrigan 1993).

Recently, however, a number of studies have emerged suggesting that brain mass rather than body mass is the primary constraint on reproductive rates. Isler and Van Schaik (2009), for example, found stronger correlations between $r_{\max}$ and brain mass than between $r_{\max}$ and body mass in a substantial sample of mammalian taxa. Since the suitability of general mammalian regression equations for the prediction of hominin $r_{\max}$ is debatable, data on $r_{\max}$ and body mass from Ross (1988) and brain volume from Stephan and colleagues (1981) were collated to provide regression equations for prediction based solely on the primate order. Brain volumes were converted to brain masses using the standard density of brain tissue at 1.036kg / litre (Snyder et al. 1975). With all variables log-transformed, multiple stepwise regressions of $r_{\max}$ on body mass and brain mass confirm the findings of Isler and Van Schaik (2009a) in that body mass is not included in the final model. However, it is inconceivable that body mass has no effect on reproductive rates, particularly in large-bodied species. Both variables index elements of the total energetic cost of growth; it is logical to hypothesize that if one could enumerate the weights of all somatic tissues, s_i, and their relative metabolic rates, m_i, for each species, then $r_{\max}$ would correlate more closely with the total metabolic cost of the organism, $\sum s_i m_i$, than with any individual somatic component. Following this logic, brain mass provides a closer correlation with $r_{\max}$ than does body mass simply because the

brain is a particularly expensive tissue (e.g. Aiello and Wheeler 1995), and body mass falls out of the multiple regression due to its close positive correlation with brain mass.

To test the possibility that brain mass and body mass have combined effects on $r_{\max}$, an equation of the form $\ln(r_{\max}) = \alpha[\ln(\text{body mass}) + \beta \ln(\text{brain mass})] + \gamma$ was fitted to the primate data, yielding a highly significant regression model. The constant β was then extracted and used to produce a compound variable, $c = \ln(\text{body mass}) + \beta \ln(\text{brain mass})$. When this compound variable was entered into a multiple stepwise regression model with body mass and brain mass, it displaced both, explaining more variance in $r_{\max}$ than brain mass alone (Brain mass: R^2 = .846, $F(1,23) = 145.817$, $p < 0.001$; Compound variable: R^2 = .865, $F(1,23) = 147.782$, $p < 0.001$), though this improvement was marginal. This relationship is depicted in Figure 2a.

The value of β in the above equation, 4.997, can be taken as a crude indication that variation in brain mass accounts for approximately five times as much variation in $r_{\max}$ than does variation in body mass within this sample. This is of considerable importance for the arguments that follow, because whilst the body masses of extant great apes are comparable to or greater than those of extant *Homo sapiens*, their brain masses are considerably smaller. If $r_{\max}$ were principally determined by body mass it would suggest that all the apes, as large-bodied primates, would have faced similar selective pressures with regard to reduced reproductive rates. Since $r_{\max}$ in fact appears to be principally determined by brain mass, this suggests that the reduction in reproductive rates experienced by ancestral hominins, particularly members of the genus *Homo*, would have been substantially greater than those experienced by the other great apes. To produce estimates of $r_{\max}$ in an appropriate hominin sample, the equation $\ln(r_{\max}) = \alpha c + \gamma$ was applied, employing body masses from Grabowski and colleagues (2015) and brain masses calculated from Grove and colleagues (2012). The estimated $r_{\max}$ values are plotted against the geological ages of the hominins for which they were estimated in Figure 2b, showing a clear decrease in intrinsic rates of increase over the 3.2 million years for which reliable samples were available.

5.3. Effects on the hominin adaptation

The preceding sections demonstrate empirically that climatic heterogeneity has increased over the past five million years and that the intrinsic rate of increase in the hominins has declined over the last three million years, primarily as a result of the trend towards greater encephalisation. The current section considers the effects of these trends for the biological fitness of an evolving lineage via the use of a simple evolutionary algorithm. Such algorithms are direct analogues of natural selection in that the fitness of individuals within a population determines the probability that they will leave descendents in the next generation. The algorithm employed here is a simplification of that presented in Grove (2014); only a brief description is offered here, as mathematical details and source code can be found in the original publication.

The algorithm involves a population of agents subject to a selection regime based purely on the fluctuating value of a putative climatic variable. It operates on a fixed population size of 1,000 individuals. Each iteration, the least fit n individuals are removed from the population to be replaced by n offspring of the fittest individuals. Fitness is determined by examining a single, continuously varying tracking 'locus', with highest fitness achieved when the absolute difference between the climatic variable and the value at this locus is equal to zero. The replacement of n individuals per generation thus enables the population to track the climatic variable. Variation is introduced into the

population via a mutation operator that employs a uniformly distributed random variable to slightly perturb the value at the tracking locus of each new offspring relative to its parent. At the start of each run, the values at the tracking locus in each agent are drawn from a Gaussian distribution with a mean equal to the climatic variable in the first iteration and a small variance. The outputs of the model are the values of the tracking locus and of the associated fitness; both are averaged over the 1,000 agents and plotted against iteration number.

This simple evolutionary algorithm is used to examine the effects of both increasing climatic heterogeneity and decreasing rates of intrinsic increase on the ability of the population to track the climatic variable. The climatic variable was modelled as a symmetrical saw-tooth curve, as this waveform echoes the cyclical nature of real palaeoclimatic data and has a constant absolute first derivative (i.e. the absolute rate of climatic change per iteration is constant). Decreasing rates of intrinsic increase are modelled by exponentially decreasing the number of individuals replaced per iteration during the course of a run, whilst climatic heterogeneity is increased by exponentially increasing the amplitude of the saw-tooth curve during the course of a run. Figure 3a provides a baseline condition in which both climatic heterogeneity and the intrinsic rate of increase are held constant throughout; in this case, the population mean (black line) tracks the climatic variable (grey line) with a minimal lag.

Figure 3b shows a result produced by holding the intrinsic rate of increase constant whilst increasing climatic heterogeneity over the course of the simulation; by the end of the run, the mean value of the tracking locus is unable to accurately track the climatic variable. Figure 3c shows a result in which climatic variability is held constant whilst decreasing the intrinsic rate of increase; again, the mean value of the tracking locus gradually strays further from the climatic variable as the simulation proceeds. Finally, Figure 3d simultaneously increases climatic heterogeneity whilst decreasing the intrinsic rate of increase over the course of the simulation; this leads to a substantial deficit in the tracking locus by the end of the run. To make these four results easier to compare, Figure 4 shows mean fitness over time for the four separate simulations, scaled such that the least fit value of any population during any simulation equals zero. The baseline condition produces almost constant fitness, whilst decreases in the intrinsic rate of increase or increases in climatic heterogeneity have similar, detrimental effects. Simultaneous increases in climatic heterogeneity and decreases in intrinsic rates of increase produce the greatest decreases in fitness over time. This latter situation is the one that most closely reflects the situation faced by evolving hominins over the last three million years.

Finally, to demonstrate directly the effects of increasing climatic heterogeneity and decreasing intrinsic rates of increase over the course of hominin evolution, two further runs of the evolutionary algorithm were implemented using the LR04 stack as the climatic to curve to which the population was attempting to adapt. The first used an intrinsic rate of increase fixed throughout at the value predicted for the oldest hominins represented in Figure 2b. The second used a linear regression fitted to all the data in Figure 2b to predict decreases in the intrinsic rate of increase through time; as before, such decreases are modelled as decreases in the number of individuals replaced per iteration during the course of a run. Figure 5a plots the LR04 curve to which the population was attempting to adapt, whilst Figure 5b plots the extent to which the fixed intrinsic rate of increase leads to fitness advantages over the empirical scenario in which the intrinsic rate decreases. As would be expected, the greatest fitness advantages occur in more recent times, when climatic

fluctuations are greater and intrinsic rates are lower. This effect is particularly marked during the rapid, near-vertical changes in climate visible in Figure 5a, most of which indicate rapid global warming events at the termination of glacial episodes. This is a highly simplified model, and Figure 5b should be viewed as a schematic only; nonetheless, it is indicative of the very real costs of reducing intrinsic rates during periods of increasing climatic heterogeneity.

6. Resolving the paradox?

Increasing climatic heterogeneity and decreasing intrinsic rates of increase in the hominins are demonstrable empirical patterns over the past three million years. The paradox that arises, therefore, is why the hominin lineage reponded to an extrinsic challenge – increasing climatic heterogeneity – by imposing an additional intrinsic challenge – the decrease in reproductive rates caused by encephalisation. The above simulations show that the combined burdens of increasing climatic heterogeneity and decreasing reproductive rates lead to a substantial deficit in the ability of the population to track environmental change. Why, then, did hominin evolution follow this trajectory?

One possible scenario is that the hominin lineage increasingly shifted the burden of adaptation onto cultural rather than biological adaptations, and that this reliance on cultural solutions required a degree of encephalisation that, as a consequence, depressed reproductive rates. The work of Isler and van Schaik, surveyed above, suggests that brain size is a major constraint on $R_{\max}$; during the course of hominin evolution, therefore, the benefits of encephalisation must have outweighed the costs of reduced reproductive rates. By contrast, the circumstances of the other great apes must have been such that the costs of reduced reproductive rates outweighed the benefits of encephalisation.

Part of the explanation for this contrast almost certainly relates to pre-existing differences in the ways that ancestral hominins and the ancestors of the other great apes responded to, and therefore experienced, climatic variability. The folivore / frugivore adaptations of the extant great apes restrict them largely to forested areas (Potts 2004), with even 'savannah chimpanzees' deriving the majority of their calories from the forested areas of their habitats (e.g. Schoeninger et al. 1999). It is likely that chimpanzees, for example, have never existed far beyond their current latitudinal range, and that they responded to Plio-Pleistocene climatic fluctuations primarily via expansion and contraction in line with the expansions and contractions of their habitat. As such, they successfully minimized the extent of climatic change that they actually experienced as a species. By contrast the hominins, from at least the times of the earliest 'transitional' members of the genus *Homo* (*H. rudolfensis, H. habilis*), appear to have developed somewhat broader tolerances, at least in dietary terms (e.g. Ungar et al. 2006).

Although contraction and expansion would still have been an essential part of the response to climatic variability, the broader diets of these species would have limited the severity of this pattern. Crucially, if ancestral hominins were thus able to retain broader latitudinal ranges during climatic downturns, they would have been exposed to novel (or at least more stringent) selective pressures along axes other than diet, particularly at the margins of their geographic range. The ability to subsist for a time on the subset of the dietary spectrum that occurs at more northerly latitudes, for example, solves the problem of what to eat, but it does not solve the problem of thermoregulation that also occurs at such latitudes. Thus greater tolerance on one axis often exposes a species to

selection for greater tolerance on other, covarying axes. This process, a variant of what is often generically referred to as 'behavioural drive' (e.g. Wyles et al. 1983; Huey et al. 2003), can amplify pre-existing differences between species under conditions of recurrent environmental fluctuation. In the case of the hominins as opposed to the other great apes, it is argued here that a greater degree of pre-existing (dietary) generalism enabled the former to survive a greater range of habitats, in the process exposing them to novel selective pressures; the increasing rates at which they were exposed to such pressures under an increasingly variable climate ensured that only advanced cognitive mechanisms, scaffolded by encephalisation, were sufficient to meet the case.

It is therefore suggested in this context that encephalisation had a direct bearing on hominin abilities to accommodate increasingly heterogeneous environments, and indeed there is evidence for positive correlations between levels of environmental variability and hominin brain size (e.g. Ash and Gallup 2007; Grove 2012). This line of reasoning suggests a bifurcation in possible strategies followed by organisms adapting to increasingly variable environments. Under increasing environmental heterogeneity a lineage with a given reproductive rate could either be selected to increase that rate, thus allowing genomic evolution to track the environment (this is the standard r / K logic), or it could be selected to increase brain size, pursuing a strategy in which environmental heterogeneity is managed via cognitive mechanisms such as learning and cultural transmission. In this latter context, r / K can be seen as a cognitive continuum describing the extent to which a species deals with its environment through either genomic or cognitive means. The place of a given species on the continuum now indexes the balance between these two possible types of solutions.

Whilst it is difficult to directly reconstruct cognitive abilities, especially in extinct species, a modelling framework proposed by Gomez-Mestre and Jovani (2013) can be used to predict the level of phenotypic plasticity likely to evolve in a population facing a given environmental regime. In a broad sense, phenotypic plasticity is simply the ability of a single genotype to produce different phenotypes under different environmental conditions. The key to understanding phenotypic plasticity in the context of human evolution is to note explicitly that behaviour is part of the phenotype, and that the phenotype thus includes processes such as learning and cultural transmission that might be facilitated by encephalisation. Although plastic phenotypic responses are variable, and many involve environmentally induced changes in gene expression that have no necessary bearing on behaviour, we can first predict the level of plasticity required in a given population, and then posit that at least a proportion of this plasticity is achieved via behavioural adaptation. Indeed, in highly encephalised species, behaviour will often be the quickest and most efficient means of dealing with environmental change.

The simulation presented below extracts the most important elements of the Gomez-Mestre and Jovani (2013) model, but does not attempt to replicate its full complexity. To introduce phenotypic plasticity into the evolutionary algorithm, we simply introduce a second locus in each individual that indexes the amount of plasticity it is capable of producing. This locus is subject to selection in exactly the same way as the other locus; at the start of the simulation, each individual has an arbitrarily small ability to produce plastic responses, and selection then acts to increase or decrease this ability as the simulation progresses. An individual uses its plasticity to shift itself closer to the environmental value encountered in a given generation. In the simulation results plotted in Figures 3 and 4, an individual's fitness is measured as the distance between its genotype and the environmental variable; in the simulation reported here, the fitness of an individual is the distance

between its *phenotype* and the environmental variable. If the value of the environmental variable is 0.5 and the value of an individual's genotype is 0.4, that individual will perfectly match the environment providing it has a plasticity level of >=0.1. Selection for plasticity should thus be stronger when individual genotypes are further from the environmental variable. To avoid runaway selection for plasticity a direct cost per unit of plasticity is applied to each individual; this depresses fitness prior to reproduction, ensuring that plasticity only evolves when it is absolutely necessary.

This modified model is used to ascertain the conditions under which plasticity will evolve, and is initially run for the same four sets of conditions as the original model, with environmental heterogeneity either constant or increasing and reproductive rates either constant or decreasing. The basic result is shown in Figure 6. As can be seen from this graph, selection for plasticity is strongest when environmental heterogeneity is increasing and reproductive rates are decreasing. This is perhaps unsurprising, given that this is the situation in which the challenges to adaptation are greatest, but it suggests that the conditions faced by the hominin lineage are exactly those in which plasticity is expected to evolve.

Finally, to demonstrate directly the effects on plasticity of increasing climatic heterogeneity and decreasing intrinsic rates of increase over the course of hominin evolution, and to make the results of this modified model directly compatible with those of the original model, two further runs of the evolutionary algorithm were implemented using the LR04 stack as the climatic to curve to which the population was attempting to adapt. The first used an intrinsic rate of increase fixed throughout at the value predicted for the oldest hominins represented in Figure 2b. The second used a linear regression fitted to all the data in Figure 2b to predict decreases in the intrinsic rate of increase through time. Figure 7 plots evolved plasticity in the scenario in which reproductive rates decrease divided by evolved plasticity in the scenario in which they are held constant. This plot demonstrates that plasticity under decreasing reproductive rates is frequently between 2 and 3 times that under constant rates after around 1.5 million years ago. When comparing this figure with Figure 5, it is clear that the greatest plasticity levels evolve when the population is least able to track the environment via non-plastic adaptation.

7. Discussion: Complex populations and complex individuals in hominin evolution

7.1. On biology and culture

Anthropologists (and indeed researchers from many other disciplines) have long grappled with the distinction between biology and culture. This is in many ways a false dichotomy, but works occasionally as a useful heuristic device. The issue becomes particularly thorny when discussion turns to plasticity, not least because plasticity may be affected via 'purely' biological means, or by some combination of biological and cultural adaptations. A canid that develops a thicker coat in cold winter temperatures but sheds that coat at the onset of spring is displaying a plastic adaptation, but no-one would assert that this adaptation is in any way cultural. At the other end of the spectrum, a hominin ancestor who constructs a shelter during the winter months but abandons it during the warmer months of the seasonal round is displaying a functionally very similar adaptation, but one that most would regard as cultural. There are two clear differences between these two examples:

1) the canid's genome contains information specifying the conditions in which the coat will alternately thicken and be shed, as well as information on how the coat will be generated; no-one would make a similar claim about the blueprint for the hominin ancestor's shelter.

2) the canid's coat is a *somatic* adaptation; the hominin ancestor's shelter is not.

The first of these differences is closest to the classic 'method of exclusion' definition of culture; something may be called cultural if it is not (empirically, cannot) be explained by recourse to genetics. The clearest recent example of this line of thinking comes from the debate surrounding cultural variation in chimpanzees, where analyses demonstrating that genetic relatedness between the three extant chimpanzee subspecies did not correspond to variation in elements of the cultural repertoire was seen as concrete evidence in favour of the 'culture hypothesis' (e.g. Lycett et al. 2009).

The second difference has been of considerable historical importance, particularly to archaeologists for whom material culture is the main proxy for prehistoric behaviour. The clearest early proponent of this approach was White (1959), who explicitly defined culture as a means of 'extra-somatic adaptation'. Indeed, many archaeologists still of necessity equate culture with *material culture*. In most archaeological circumstances we can be relatively sure that material culture is in fact a manifestation of culture more broadly construed, but there are many examples from other species that muddy the waters somewhat. A spider's web, for example, is extra-somatic, but is not cultural; the clasping of an overhead branch or a partner's hand while grooming in chimpanzees are clearly variants maintained via cultural tradition, yet neither leaves an extra-somatic record. Thus culture need not be extra-somatic, and the production of extra-somatic structures need not be cultural.

The use of 'cultural' as a synonym for 'non-biological' does, however, map onto what is perhaps the most important operational distinction between biology and culture: that culture can enable adaptation to a given environment to occur *faster* than would biological adaptation. This is a distinction not about the physical manifestations of culture (where they exist), but about the mechanisms by which they are transmitted between individuals. If a fitness-conferring behaviour can be learnt from parents or peers soon after its initial innovation, that behaviour can spread through the population far faster than could any fitness-conferring gene. This may be a general principle, but it is of particular value to long-lived, slowly reproducing species such as the hominins. Thus we return to the critical life history axis that runs throughout the analyses detailed above; there is good reason to believe that biologically 'slow' species will benefit far more from cultural adaptations than will biologically 'fast' species. The most important way in which culture benefits 'slow' species is in facilitating greater plasticity, thereby enabling adaption to environmental changes *during the lifetime of the individual*.

7.2. Manifestations of plasticity in human evolution

The fossil and archaeological records of human evolution both provide evidence of plasticity. I focus here on the archaeology, however, since plasticity is something of a burden to the physical anthropologist. Anatomical plasticity has a tendency to cloud taxonomic analysis, to the extent that a highly plastic species is more likely to be referred to as a series of different species rather than one highly plastic one. This is particularly the case when variation is regional: on the one hand, where regions differ in environmental variables we would expect a plastic species to produce different

morphs; on the other, correlations between morphological and geographical distances are often seen *prima facie* as evidence of allopatric speciation.

Many components of an archaeological assemblage may be regarded as evidence of the plasticity of their makers. Elements of the toolkit that provide access to previously unavailable food sources broaden the possible subsistence base, and may equip hominins to respond adaptively to the seasonal ebb and flow of available foods. On a broader timescale, there is increasingly robust evidence that the dispersal of *Homo sapiens* out of Africa after 100 ka was facilitated by the use of a particularly plastic toolkit (Grove et al. 2015). The models presented above concentrate on environmental heterogeneity over time, with an implicit assumption that the changes depicted are experienced within a given region. Dispersal creates a situation in which individuals encounter environmental heterogeneity over time due to relocation and may be an ideal situation in which to examine manifestations of plasticity. Dispersal poses two main problems for a hominin in terms of toolkit selection: both the potential subsistence base and the locations of future raw material sources are unknown. Binford (1976) postulated that longer forays from a known base were likely to involve a greater array of tasks due to the increasing array of potential resources encountered. A greater array of tasks, he noted, would require either a large number of task-specific tools or a small number of multi-purpose tools. In the parlance of the current paper, we can refer to this latter solution as the use of plastic tools, or of a plastic toolkit.

The maintenance of a plastic toolkit is clearly the more beneficial of Binford's two solutions, not least because it has the advantage of reducing carrying costs. As Ambrose (2010:141) has observed, "mobile foragers would be excessively burdened if they had to carry the right tool for every possible task". Nonetheless, they must be equipped as well as possible for every possible task, hence the likely reliance on "generalized, durable, transformable tools" (Ambrose 2010:141). The lack of information regarding new sources of raw material should also have encouraged dispersing hominins to conserve materials where possible, suggesting that what was needed was a tool form that was both multi-functional in itself and useable as a source of raw material for the production of new tools. Independently, researchers examining both the dispersal of *Homo sapiens* out of Africa and the colonisation of the Americas have noted that thick bifacial tools (literally, tools from which flakes have been removed from both sides) would ideally suit this purpose. Parry and Kelly (1987) argue that bifacial reduction is a direct response to unpredictable environments, with Kelly and Todd (1988:237) further noting that bifacial tools are capable of "long, variable use-lives". When blunted, such tools can be easily re-sharpened; their weight and thickness mean that they can also act as cores (that is, they can be used effectively as sources of raw material for the production of smaller flake tools). The first colonisers of the Americas, and the first *Homo sapiens* to leave Africa, both carried thick bifacial flakes and points of this type. It seems likely, therefore, that they were combating a lack of information about the environmental changes that they might encounter via recourse to a highly plastic toolkit.

There are also a series of somewhat simpler – though less clearly dated – examples of hominins offloading somatic adaptations so as to facilitate adaptation to environmental change through what might be considered plastic means. Many of these are directly comparable to the example of shelter construction given above. It is likely, for example, that earlier hominins (and indeed many later ones) used natural structures as shelters rather than constructing their own. Caves are the classic and by far the most numerous example; it is notable in this context that, in a study of cave use by chacma

baboons, Barrett and colleagues (2004) demonstrated that the temperature inside a cave remains largely constant despite daily fluctuations in temperature in the surrounding environment. Cave use thus acts as a homeostatic mechanism for extant primates in much the way that we can infer it once did for hominins. Other external homeostatic mechanisms of this kind include the development of clothing and the use of fire.

7.3. Complex populations of complex individuals

In chapter 9 of CFMN, Godfrey-Smith considers two quite different solutions to the problem of environmental complexity: the complexity of a population, and the complexity of individuals. Complexity here is once again understood as heterogeneity. We can think of two 'strategies' available to an individual, and a further two available at the population level; in both cases, these strategies can be characterised as homogeneity and heterogeneity. When there is intra-individual homogeneity, each individual produces a fixed response, irrespective of the environment it encounters. Where intra-individual heterogeneity exists, individuals respond in different ways to different environments. When there is inter-individual homogeneity, all members of a population produce the same response to a given environment. Finally, when inter-individual heterogeneity exists, there is a diversity of responses to a given environment within the population. Note that a population may be either homogenous or heterogeneous regardless of whether intra-individual homogeneity or intra-individual heterogeneity obtains. These alternatives provide a 2 by 2 matrix of four possible solutions, of which Godfrey-Smith focuses on two: complex populations of simple individuals and simple populations of complex individuals. He shows, via an argument based on the Levins model (Levins 1968), that there are certain circumstances under which a simple population of complex individuals will out-compete a complex population of simple individuals. This is essentially because although population-level heterogeneity can increase the fitness of the population, individual-level heterogeneity can increase the fitness of the individual; a set of fitter individuals leads to a fitter population, but the converse does not hold (indeed, arguments based on polymorphisms and bet-hedging 'sacrifice' many individuals by producing a wide variety of phenotypes, only some of which will survive).

Phenotypic plasticity explicitly concerns the complexity of individuals; in many of the archaeological examples discussed above it is rapidly reversible, meaning that an individual can switch between two states an almost infinite number of times during its lifetime. The models employed above reveal an additional by-product of the evolution of plasticity, which is obvious only in retrospect. Provided the costs of plasticity are not too high, a lineage will tend to use plasticity to adapt to rapidly changing environments rather than doing so via the genotype directly. As plasticity evolves, the phenotype continues to track the environment whilst selection on the genotype is relaxed; in the saw-tooth environments employed in the models above, the genotype gradually settles towards a trajectory which follows the long-term mean of the environmental states it encounters. A by-product of this relaxed selection on the genotype is that the plastic population demonstrates far greater genotypic diversity than does the non-plastic population. The result is shown in Figure 8.

This outcome has interesting implications for the relationship between individual and population-level complexity. Godfrey-Smith's (1996) conclusions suggested that simple populations of complex individuals will out-compete complex populations of simple individuals in certain circumstances. The result depicted in Figure 8 suggest that complex individuals – as indexed by the presence of

phenotypic plasticity – tend to exist in complex populations *as a result of their individual complexity*. Provided the environment is sufficiently heterogeneous over evolutionary time, plasticity will be a beneficial adaptation, and could lead to standing genotypic diversity that may itself become valuable under circumstances of sudden environmental change.

To conclude this section, I briefly survey an example of the distinction between homogeneity and heterogeneity in individuals and populations that bears directly upon human evolution. Gamble (1997) has proposed a series of 'break points' in human evolution relating to the anatomy of ancestral hominins and the lithic technologies with which they were equipped. The treatment below expands his initial schema and relates the break points to changes in individual or population-level complexity. In his 'Pre-Palaeolithic' period (i.e. the period before the first advent of stone tools), Gamble envisages African hominins having morphological adaptations that enable them to inhabit relatively circumscribed niches; they are specialists in the sense that their tolerance of environments beyond these niches is relatively limited. In Godfrey-Smith's terms individuals are simple, and there is limited differentiation within populations, leading to overall simplicity at the population level also. In the 'Earlier Palaeolithic' period, which encompasses the Lower Palaeolithic and a good proportion of the Middle Palaeolithic in traditional parlance, hominins spread throughout the Old World (after 2 Ma) on the basis of a generalist morphology. They were accompanied by a generalist lithic technology for the majority of the period, but were still bound by their ecology, at least at the continental scale; as the African biome stretched into Asia, for example, they expanded with it, but were in turn forced to retract as environmental conditions deteriorated. Individuals were generalists, but generalism (unlike plasticity) is a fixed response, so individuals were still relatively simple. There is an increase in population-level plasticity towards the end of this period, however, because the ebb and flow of populations frequently mixed temporarily separated groups, with both genetic and cultural adaptations shared as a result. Technologies arising in the environmental extremes of a species' range thus became integrated into the cultural repertoire, paving the way for subsequent developments.

Finally, in the 'Later Palaeolithic', the burden of adaptation is shifted further from the biological to the cultural, with a global distribution of hominins adapting to specific localities via their technologies rather than being constrained to specific habitats by their biology. To paraphrase Lahr and Foley (1998), this is the phase during which hominins finally tip the balance from a dominant pattern of expanding *with* their traditional habitat to one in which expanding *beyond* their traditional habitat becomes pervasive. Individuals are now fully plastic, and therefore complex, due mainly to the speed at which their technologies allow them to accommodate environmental change. Populations are also complex, with evidence for specialisation in the production of specific tool forms and at least putative evidence for divisions of labour on the basis of both age and sex.

This schematic presentation is not intended to suggest that these transitions were discrete, nor even necessarily rapid; rather, it locates the broad chronological locations of the changes that are here considered important in assessing the extent of individual and population level complexity. Factors beyond those of morphology, technology, and geography remain important, but many of their effects arise directly from the interactions of these variables. Increasingly plastic individuals, for example, form populations that traverse and colonise habitats that were once inaccessible to them, reducing fragmentation and creating corridors between previously isolated groups. The resulting interconnections create opportunities for both genetic and cultural exchange (Powell et al. 2009;

Grove 2016), with the latter increasing further the possibilities of innovation and cultural elaboration that stand as a hallmark of the human species.

8. Conclusions

This paper began by summarising the important parallels between the central themes of CFMN and those that currently absorb evolutionary anthropologists studying the interface between palaeoclimatic variability and human evolution. The ECT is a framework that deserves to be more closely integrated with such research; indeed, both theoretical arguments and empirical results arising from evolutionary anthropology closely shadow, and in many cases complement, those put forward in CFMN. Palaeoanthropological treatments of human cognitive evolution necessarily focus on gross brain size as the key variable, though there is convincing – and increasing – evidence that this genuinely provides a useful proxy for cognitive abilities. The analyses reported above focus on three main trends: the increase in palaeoclimatic heterogeneity, the increase in hominin encephalisation, and the decrease in hominin reproductive rates. The latter two are intimately related within the wider setting of hominin life history evolution.

The decrease in hominin reproductive rates, when coupled with the increase in palaeoclimatic heterogeneity, produced a considerable deficit in the ability of the hominin lineage to track changing environmental conditions. It is argued that this deficit was accommodated via an increase in phenotypic plasticity in the hominin lineage, and that this is manifest particularly in the increasing complexity of material culture. Finally, it is suggested that major 'break points' in human evolution can be usefully related to Godfrey-Smith's (1996) notion of individual and population-level complexity. Plastic individuals are necessarily complex, but it is argued that this individual-level complexity, particularly when it results in rapid cultural evolution, automatically results in population-level complexity via relaxed selection on the genotype.

References

Aiello LC, Dunbar RIM (1993) Neocortex size, group size, and the evolution of language Current Anthropology 34:184-193 doi:10.1086/204160

Aiello LC, Wheeler P (1995) The expensive tissue hypothesis - the brain and the digestive system in human and primate evolution Current Anthropology 36:199-221 doi:10.1086/204350

Ambrose SH (2010) Coevolution of Composite-Tool Technology, Constructive Memory, and Language Implications for the Evolution of Modern Human Behavior Current Anthropology 51:S135-S147 doi:10.1086/650296

Ash J, Gallup GG, Jr. (2007) Paleoclimatic variation and brain expansion during human evolution Human Nature-an Interdisciplinary Biosocial Perspective 18:109-124 doi:10.1007/s12110-007-9015-z

Barrett L, Gaynor D, Rendall D, Mitchell D, Henzi SP (2004) Habitual cave use and thermoregulation in chacma baboons (Papio hamadryas ursinus) Journal of Human Evolution 46:215-222 doi:10.1016/j.jhevol.2003.11.005

Binford LR Forty-seven trips: A case study in the character of some formation processes of the archaeological record. In: Hall ES (ed) Contributions to Anthropology: The Interior Peoples of Northern Alaska. National Museum of Man, Ottawa, pp 299-351

Boyd R, Richerson P (1985) Culture and the Evolutionary Process. University of Chicago Press, Chicago

Bromham L, Rambaut A, Harvey PH (1996) Determinants of rate variation in mammalian DNA sequence evolution Journal of Molecular Evolution 43:610-621 doi:10.1007/bf02202109

Charnov EL, Berrigan D (1993) Why do female primates have such long lifespans and so few babies? or Life in the slow lane Evolutionary Anthropology 1:191-194 doi:10.1002/evan.1360010604

DeMenocal PB (2004) African climate change and faunal evolution during the Pliocene-Pleistocene Earth and Planetary Science Letters 220:3-24 doi:10.1016/s0012-821x(04)00003-2

Dunbar RIM (1998) The social brain hypothesis. Evolutionary Anthropology 6:178-190 doi:10.1002/(sici)1520-6505(1998)6:5<178::aid-evan5>3.0.co;2-8

Gamble CS (1997) The skills of the Lower Palaeolithic Proceedings of the Prehistoric Society 63:407-410

Godfrey-Smith P (1996) Complexity and the Function of Mind in Nature. Cambridge University Press, Cambridge.

Gomez-Mestre I, Jovani R (2013) A heuristic model on the role of plasticity in adaptive evolution: plasticity increases adaptation, population viability and genetic variation Proceedings of the Royal Society B-Biological Sciences 280 doi:10.1098/rspb.2013.1869

Grabowski M, Hatala KG, Jungers WL, Richmond BG (2015) Body mass estimates of hominin fossils and the evolution of human body size Journal of Human Evolution 85:75-93 doi:10.1016/j.jhevol.2015.05.005

Grove M (2011a) Change and variability in Plio-Pleistocene climates: modelling the hominin response Journal of Archaeological Science 38:3038-3047 doi:10.1016/j.jas.2011.07.002

Grove M (2011b) Speciation, diversity, and Mode 1 technologies: The impact of variability selection Journal of Human Evolution 61:306-319 doi:10.1016/j.jhevol.2011.04.005

Grove M (2012a) Amplitudes of orbitally induced climatic cycles and patterns of hominin speciation Journal of Archaeological Science 39:3085-3094 doi:10.1016/j.jas.2012.04.023

Grove M (2012b) Orbital dynamics, environmental heterogeneity, and the evolution of the human brain Intelligence 40:404-418 doi:10.1016/j.intell.2012.06.003

Grove M (2014) Evolution and dispersal under climatic instability: a simple evolutionary algorithm Adaptive Behavior 22:235-254 doi:10.1177/1059712314533573

Grove M, Lamb H, Roberts H, Davies S, Marshall M, Bates R, Huws D (2015) Climatic variability, plasticity, and dispersal: A case study from Lake Tana, Ethiopia Journal of Human Evolution 87:32-47 doi:http://dx.doi.org/10.1016/j.jhevol.2015.07.007

Grove M (2016) Population density, mobility, and cultural transmission. Journal of Archaeological Science 74:75-84 doi:10.1016/j.jas.2016.09.002
Grove M, Pearce E, Dunbar RIM (2012) Fission-fusion and the evolution of hominin social systems Journal of Human Evolution 62:191-200 doi:10.1016/j.jhevol.2011.10.012
Hart TB, Hart JA (1986) The ecological basis of hunter-gatherer subsistence in African rain forests: the Mbuti of Eastern Zaire Human Ecology 14:29-55 doi:10.1007/bf00889209
Harvey PH, Clutton-Brock TH (1985) Life-history variation in primates Evolution 39:559-581 doi:10.2307/2408653
Hays JD, Imbrie J, Shackleton NJ (1976) Variation in Earth's orbit - pacemaker of ice ages Science 194:1121-1132 doi:10.1126/science.194.4270.1121
Hennemann WW (1983) Relationships among body mass, metabolic rate and the intrinsic rate of natural increase in mammals Oecologia 56:104-108 doi:10.1007/bf00378224
Huey RB, Hertz PE, Sinervo B (2003) Behavioral drive versus Behavioral inertia in evolution: A null model approach. American Naturalist 161:357-366 doi:10.1086/346135
Isler K, Van Schaik CP (2009a) Why are there so few smart mammals (but so many smart birds)? Biology Letters 5:125-129 doi:10.1098/rsbl.2008.0469
Isler K, van Schaik CP (2009b) The Expensive Brain: A framework for explaining evolutionary changes in brain size Journal of Human Evolution 57:392-400 doi:10.1016/j.jhevol.2009.04.009
Kelly RL, Todd LC (1988) Coming into the country: early Paleoindian hunting and mobility American Antiquity 53:231-244 doi:10.2307/281017
Kingston JD (2007) Shifting Adaptive Landscapes: Progress and Challenges in Reconstructing Early Hominid Environments. In: Stinson S (ed) Yearbook of Physical Anthropology, Vol 50, vol 50. Yearbook of Physical Anthropology. pp 20-58. doi:10.1002/ajpa.20733
Lack D (1954) The Natural Regulation of Animal Numbers. Clarendon Press, Oxford
Lahr MM, Foley RA (1998) Towards a theory of modern human origins: Geography, demography, and diversity in recent human evolution. In: Ruff C (ed) Yearbook of Physical Anthropology, Vol 41 - 1998, vol 41. Yearbook of Physical Anthropology. pp 137-176
Levins R (1968) Evolution in Changing Environments. Princeton University Press, Princeton
Lisiecki LE, Raymo ME (2005) A Pliocene-Pleistocene stack of 57 globally distributed benthic delta O-18 records Paleoceanography 20 doi:10.1029/2004pa001071
Lycett SJ, Collard M, McGrew WC (2009) Cladistic analyses of behavioural variation in wild Pan troglodytes: exploring the chimpanzee culture hypothesis Journal of Human Evolution 57:337-349 doi:10.1016/j.jhevol.2009.05.015
MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton
Maslin MA, Trauth MH (2009) Plio-Pleistocene East African pulsed climate variability and its influence on early human evolution. The first humans: origin and early evolution of the genus Homo. Contributions from the Third Stony Brook Human Evolution Symposium and Workshop October 3 - October 7, 2006. [Vertebrate Paleobiology and Paleoanthropology Series.]. doi:10.1007/978-1-4020-9980-9_13
McGrew WC (1992) Chimpanzee Material Culture: Implications for Human Evolution. Cambridge University Press, Cambridge
McHenry HM (1992) Body size and proportions in early hominids American Journal of Physical Anthropology 87:407-431 doi:10.1002/ajpa.1330870404
Millar JS (1977) Adaptive features of mammalian reproduction Evolution 31:370-386 doi:10.2307/2407759
Nabholz B, Glemin S, Galtier N (2008) Strong variations of mitochondrial mutation rate across mammals - the longevity hypothesis Molecular Biology and Evolution 25:120-130 doi:10.1093/molbev/msm248
Parry WJ, Kelly RL (1987) Expedient core technology and sedentism. In: Johnson JK, Morrow CK (eds) The Organization of Core Technology. Westview Press, Boulder, pp 285-304

Pianka ER (1970) On r- and K-selection American Naturalist 104:592-597 doi:10.1086/282697
Potts R (1996) Humanity's Descent: The Consequences of Ecological Instability. William Morrow, New York.
Potts R (1998) Variability selection in hominid evolution Evolutionary Anthropology 7:81-96 doi:10.1002/(sici)1520-6505(1998)7:3<81::aid-evan3>3.0.co;2-a
Potts R (2004) Paleoenvironmental basis of cognitive evolution in great apes. American Journal of Primatology 62:209-228 doi:10.1002/ajp.20016
Powell A, Shennan S, Thomas MG (2009) Late Pleistocene Demography and the Appearance of Modern Human Behavior. Science 324:1298-1301 doi:10.1126/science.1170165
Pruetz JD, Bertolani P (2007) Savanna chimpanzees, Pan troglodytes verus, hunt with tools Current Biology 17:412-417 doi:10.1016/j.cub.2006.12.042
Pruetz JD, Marchant LF, Arno J, McGrew WC (2002) Survey of savanna chimpanzees (Pan troglodytes verus) in southeastern Senegal American Journal of Primatology 58:35-43 doi:10.1002/ajp.10035
Reader SM, Hager Y, Laland KN (2011) The evolution of primate general and cultural intelligence Philosophical Transactions of the Royal Society B-Biological Sciences 366:1017-1027 doi:10.1098/rstb.2010.0342
Robson SL, Wood B (2008) Hominin life history: reconstruction and evolution Journal of Anatomy 212:394-425 doi:10.1111/j.1469-7580.2008.00867.x
Ross C (1988) The intrinsic rate of natural increase and reproductive effort in primates Journal of Zoology 214:199-219
Ross C (1992) Environmental correlates of the intrinsic rate of natural increase in primates Oecologia 90:383-390 doi:10.1007/bf00317695
Sacher GA (1959) Relation of Lifespan to Brain Weight and Body Weight in Mammals. In: Wolstenholme GEW, O'Conner M (eds) Ciba Foundation Symposium On The Lifespan of Animals, Vol. 5. John Wiley & Sons Ltd, Chichester, pp 115-141
Sacher GA (1978) Longevity and aging in vertebrate evolution Bioscience 28:497-501 doi:10.2307/1307295
Sacher GA, Staffeldt EF (1974) Relation of gestation time to brain weight for placental mammals: implications for theory of vertebrate growth American Naturalist 108:593-615 doi:10.1086/282938
Schoeninger MJ, Moore J, Sept JM (1999) Subsistence strategies of two "savanna" chimpanzee populations: The stable isotope evidence. American Journal of Primatology 49:297-314 doi:10.1002/(sici)1098-2345(199912)49:4<297::aid-ajp2>3.0.co;2-n
Shannon CE (1948) A mathematical theory of communication Bell Systems Technical Journal 27:379-423 & 623-656
Shultz S, Dunbar RIM (2010) Species Differences in Executive Function Correlate With Hippocampus Volume and Neocortex Ratio Across Nonhuman Primates Journal of Comparative Psychology 124:252-260 doi:10.1037/a0018894
Snyder WS, Cook MJ, Nasset ES, Karhausen LR, Howells GP, Tipton IH (1975) Report of the Task Group on Reference Man. Pergamon, Oxford
Stephan H, Frahm H, Baron G (1981) New and revised data on volumes of brain structures in insectivores and primates Folia Primatologica 35:1-29 doi:10.1159/000155963
Trauth MH et al. (2010) Human evolution in a variable environment: the amplifier lakes of Eastern Africa Quaternary Science Reviews 29:2981-2988 doi:10.1016/j.quascirev.2010.07.007
Ungar PS, Grine FE, Teaford MF (2006) Diet in early Homo: A review of the evidence and a new model of adaptive versatility Annual Review of Anthropology 35:209-228 doi:10.1146/annurev.anthro.35.081705.123153
Watts DP, Mitani JC (2002) Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda International Journal of Primatology 23:1-28 doi:10.1023/a:1013270606320

Western D (1979) Size, life-history and ecology in mammals African Journal of Ecology 17:185-204 doi:10.1111/j.1365-2028.1979.tb00256.x

White L (1959) The Evolution of Culture: The Development of Civilization to the Fall of Rome. McGraw-Hill, New York

White TD et al. (2009) Macrovertebrate Paleontology and the Pliocene Habitat of *Ardipithecus ramidus* Science 326:87-93 doi:10.1126/science.1175822

Wyles JS, Kunkel JG, Wilson AC (1983) Birds, behavior, and anatomical evolution. Proceedings of the National Academy of Sciences of the United States of America 80:4394-4397 doi:10.1073/pnas.80.14.4394

Figure Captions

Figure 1: Climatic heterogeneity increases over time. A) shows normalised histograms of frequencies of Benthic $\delta^{18}O$ ‰ values arranged vertically, per 5 thousand year interval. B) shows the Shannon index of heterogeneity over time at the same scale.

Figure 2. Hominin reproductive rates have decreased over time. A) shows the regression of $R_{\max}$ on a compound body and brain size variable for the hominin sample. B) shows the predicted evolution of $R_{\max}$ in the hominin lineage based on hominin body and brain mass estimates and the regression equation derived in (A).

Figure 3. Results of the evolutionary algorithm simulations. A) shows the situation in which environmental heterogeneity and reproductive rates are both held constant; B) the situation in which heterogeneity increases and reproductive rates remain constant; C) the situation in which heterogeneity remains constant but reproductive rates decrease; D) the situation in which heterogeneity increases and reproductive rates decrease. In each example the environmental trajectory is shown in grey, with the population mean genotype shown in black.

Figure 4. Fitnesses of the four trajectories shown in Figure 3 averaged per period of the saw-tooth wave.

Figure 5. Result of running the evolutionary algorithm with the LR04 stack as the environmental signal. A) shows the LR04 stack, B) shows the extent to which holding reproductive rates constant at the estimated 3.5 Ma value would have increased fitness relative to the estimated pattern of decreasing reproductive rates shown in Figure 2b.

Figure 6. Levels of plasticity evolving under the modified evolutionary algorithm for the same environmental heterogeneity / reproductive rate combinations shown in Figure 4.

Figure 7. A plot of the difference in plasticity evolving under the empirical scenario in which $R_{\max}$ decreases as per Figure 2b and the constant scenario in which Rmax is held constant at the inferred level for 3.5 million year old hominins. The environment to which the algorithm is adapting is again that graphed in Figure 5a.

Figure 8. The upper panel shows the environment to which the populations are adapting, as well as the trajectories of the mean genotype of non-plastic individuals, and the mean genotype and phenotype of plastic individuals. The middle panel shows all 1,000 genotypes of individuals in the non-plastic population through time. The lower panel shows all 1,000 genotypes of individuals in the plastic population through time. Greater genotypic diversity is demonstrated via a greater vertical spread of genotypes.

Table Captions

Table 1. Gamble's (1997) 'break points' related to individual and population-level complexity.

Technological Paradigm	Pre-Palaeolithic (5-3.3 Ma)	Earlier Palaeolithic (3.3-0.3 Ma)	Later Palaeolithic (0.3 Ma – present)
Ecological Adaptation	*Specialists* Biological	*Generalists* Biological / Cultural	*Specialists* Cultural / Biological
Skills	Habitat-specific	Generic, transferable	Place-specific
Geographical Range	Africa	Old World	Global

Figures

Figure 1

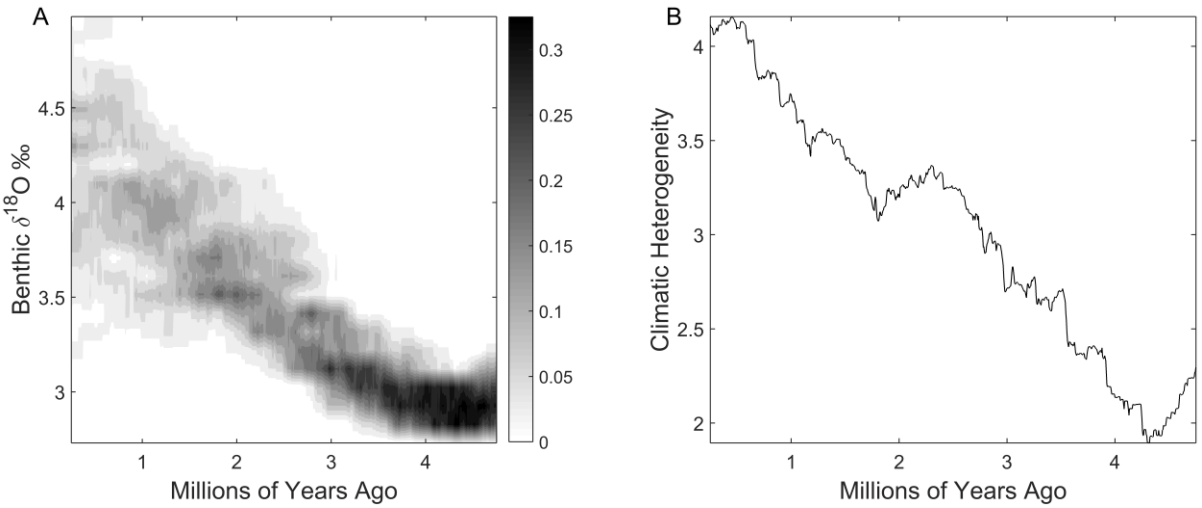

Figure 2

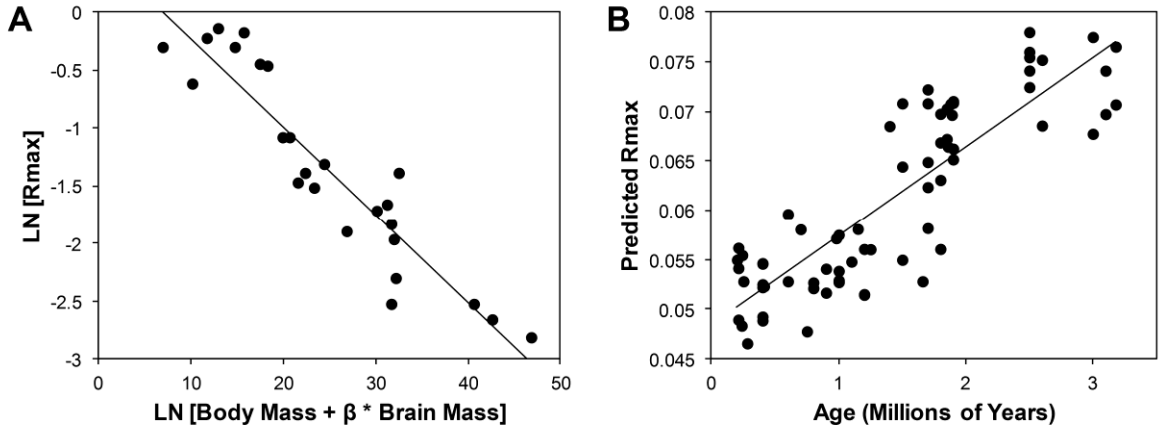

Figure 3

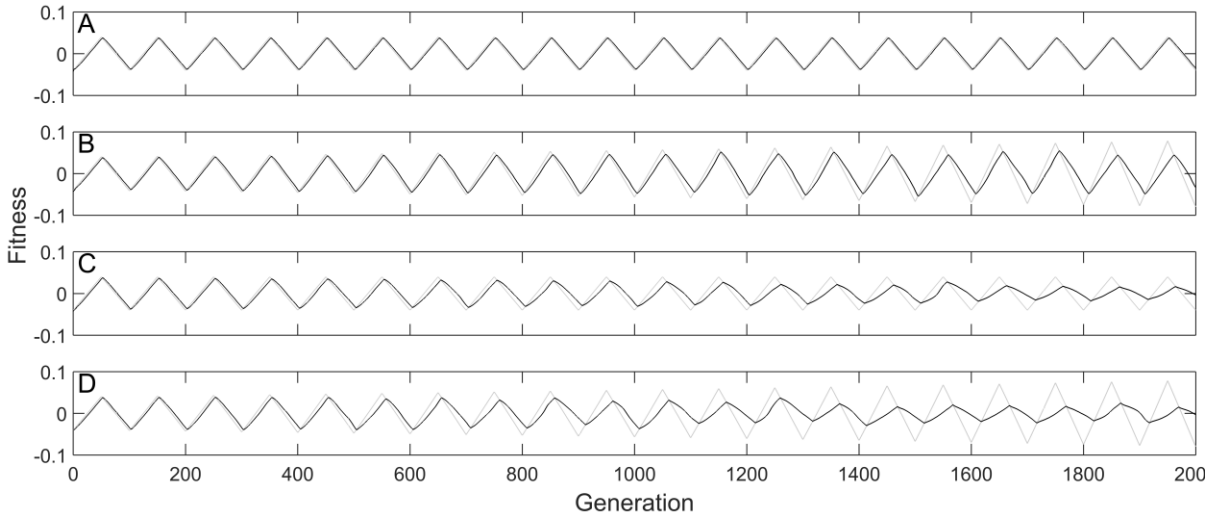

Figure 4

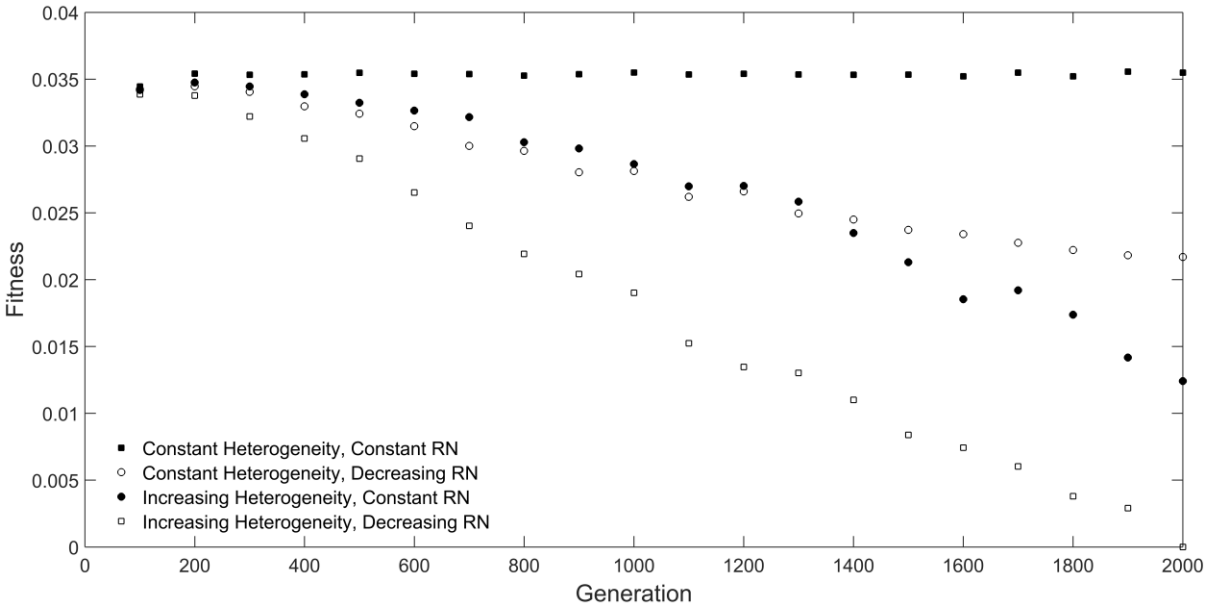

Figure 5

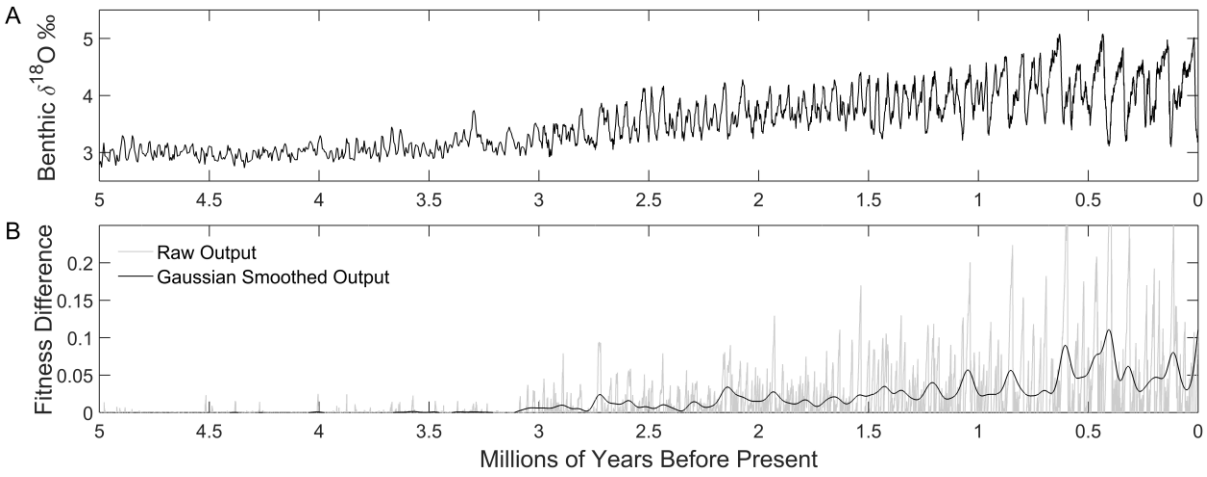

Figure 6

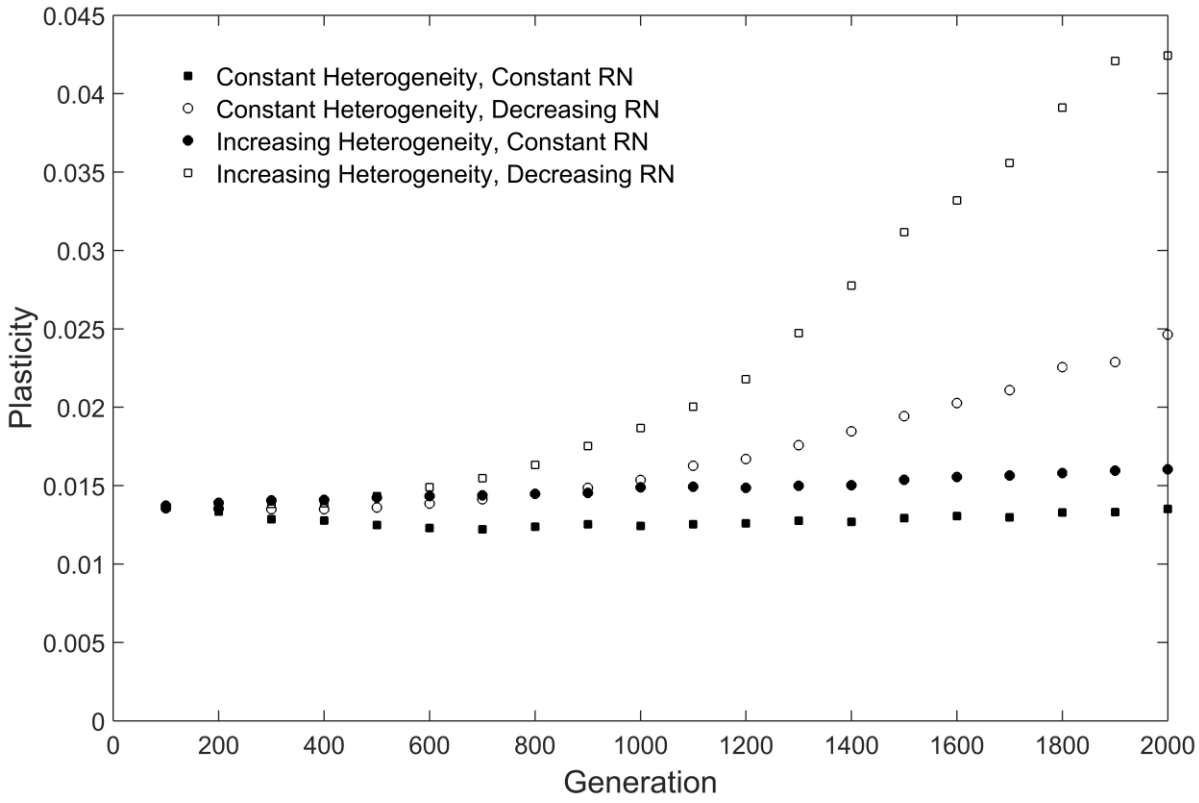

Figure 7

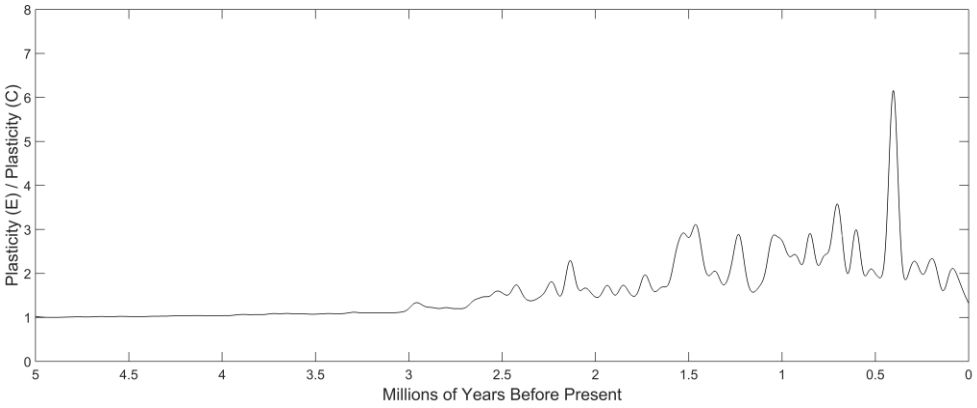

Figure 8